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Impact assessment of multiple pressures on ecosystem services with a state and transition model: Application to *Posidonia oceanica* seagrass meadows

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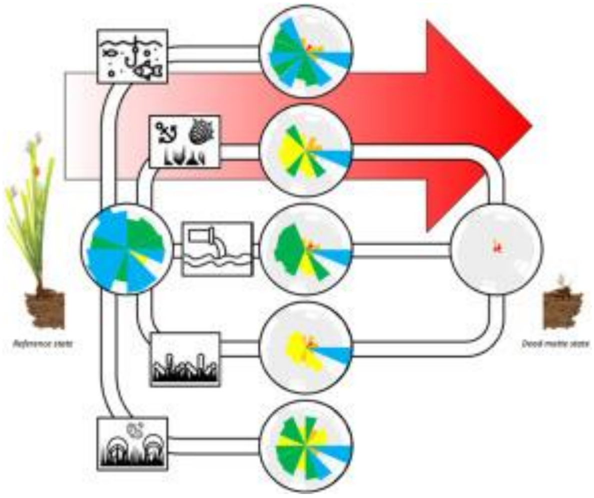
Abstract :

A significant challenge in the integration of ecosystem services into decision-making processes lies in effectively capturing the dynamics of marine socio-ecological systems, including their evolutionary pathways, equilibrium states, and tipping points. This paper explores the evolutionary trajectories of a vital marine ecosystem endemic to the Mediterranean Sea: the Posidonia oceanica seagrass meadows, in response to various drivers of change. A state-and-transition model is employed to assess the ecosystem services provided by P. oceanica across different states defined by selected transitions, such as overfishing, fragmentation, pollution, and invasion by non-native species. To apply this model, scientific expertise is combined with field data generated using the Ecosystem-Based Quality Index to evaluate the conservation status of P. oceanica. This integrated approach allows for the representation of the ecosystem services offered by the meadows across different states, leveraging ecological data. The findings highlight the disproportionate impact on provisioning services, particularly sea urchins and commercial fish production, which suffer the most under various stressors. Notably, when these services decline to critical levels, the meadows cease to provide significant benefits. Finally, a synthesized representation is presented, merging ecological insights with monitoring data, offering a framework that is more accessible to stakeholders and decision-makers.

Graphical abstract



Highlights

► Different anthropogenic pressures drive *P. oceanica* meadows into different degraded states. ► Provisioning services are the most affected services in degraded states. ► In the dead matte, the habitat becomes unable to provide any significant ES.

Keywords : Mediterranean sea, Posidonia seagrass meadows, Coastal ecosystem services assessment, Ecosystem-based quality index, Expert knowledge, Ecosystem-based approach

1 Introduction

The Ecosystem Services (ES) approach is a knowledge production process to support decisions promoting nature conservation (TEEB, 2010). It originates in the context of the biodiversity erosion crisis since the 2000s (Mace, 2014). In the history of science, focusing on the relationship between nature and human societies, the emergence of the ES approach marks a break between the dominant vision of a nature seen as a stock to manage and the emerging vision of a nature to be protected for itself and for its role in the well-being of societies (Armsworth and Roughgarden, 2001). The ES approach thus aims to make us switch to the paradigm of conservation while maintaining an assumed anthropocentric posture (Boudouresque et al., 2020a).

The ES framework proposes to analyse the interactions between living components (human and non-human) which requires a rigorous approach within different scientific disciplines to both describe the ES and understand its scope. It leads to a diversity of scientific practices: the study of the functional traits underlying ES by the ecologist (*e.g.* Hanisch et al., 2020; Tavares et al., 2019), the assessment of the individual and collective benefits obtained from ES by the economist (*e.g.* Bareille et al., 2020; Wilhelm et al., 2020), the social representations of ES by the anthropologist (*e.g.* Levine et al., 2017; Schnegg et al., 2014), the spatial analysis of ES by the geographer (*e.g.* Drakou et al., 2018; Orsi et al., 2020), etc. Ecosystem Services can therefore be defined as a boundary object that improves interactions between disciplines but also between scientists and politicians (Abson et al., 2014). Indeed, the ES approach also helps to redefine the debates between economic development and biodiversity conservation (Braat and de Groot, 2012).

Within marine sciences, the ES approach continues to develop and, from an operational perspective, promote the conservation and sustainable use of marine socio-ecological systems (Chakraborty et al., 2020). This objective is an important issue regarding the major socio-economic challenges to be taken up such as the growing demographic pressure in coastal areas, blue growth and the implementation of an international governance (Rudolph et al., 2020). However, marine and coastal ecosystems are subject to particularly strong dynamics of change: destruction and modification of habitats, pollution, overexploitation of resources, climate change, proliferation of non-native species, etc. It is estimated that 40% of the marine and coastal areas are already showing signs of degradation (IPBES, 2019). Mainly responsible for this degradation, human societies are experiencing a backlash due to the qualitative and quantitative changes in the ES bundles provided by marine and coastal ecosystems (IPBES, 2019; Kermagoret et al., 2019).

The politics and decision makers will to reverse this degradation trend is reflected in different programs and policies such as the United Nations Sustainable Development Goals by 2030 and more specifically its objective 14 “Conserve and sustainably use the oceans, seas and marine resources for sustainable development” or the United Nations Decade of Ocean Sciences for Sustainable Development (2021-2030). These examples also attest to the political will to rely on interdisciplinary scientific expertise for decision-making (Ryabinin et al., 2019). However, this scientific expertise is still under construction and it has to face challenges for producing useful knowledge for public policies (Drakou et al., 2017). Regarding the scientific approach, a major challenge is to go beyond the analyses carried out separately by each discipline and to conduct integrated studies on the same question or within the same analysis framework (Bennett, 2017). From an empirical perspective, a major challenge is to analyse the interactions between natural and social systems to better understand the functioning of marine socio-ecological systems and to be able to identify their evolutionary trajectories, their equilibrium states and their tipping points (Conversi et al., 2015; Österblom et al., 2017).

Based on the ES framework, this study explores the evolutionary trajectories of a marine ecosystem endemic to the Mediterranean Sea, the *Posidonia oceanica* (L.) Delile seagrass meadows, regarding different drivers of change. The *P. oceanica* seagrass is an ecosystem engineer species that benefits from several protection devices with regards to its high vulnerability to anthropogenic pressures (Boudouresque et al., 2012, 2009; Telesca et al., 2015). A state and transition model is applied to describe the evolution of the ecosystem capacity to provide an ES bundle regarding different anthropic pressures. The approach is original insofar as it integrates existing ecological data and expert knowledge to meet an operational demand from environmental managers through the ES framework.

2 Materials and methods

2.1 Case study: the *Posidonia oceanica* seagrass meadows of Provence and the French Riviera

P. oceanica is a Magnoliophyta dwelling in the infralittoral (up to 40 m deep) and it is endemic to the Mediterranean. Its leaves can reach over one meter in length and its rhizomes and roots constitute the so-called “matte”, *i.e.* a network filled by sediment, which can reach several meters thick and rot-proof during centuries (Boudouresque et al., 2016; Molinier and Picard, 1952; Monnier et al., 2021). *P. oceanica* seagrass meadows constitute a habitat for numerous species belonging to various functional groups (primary producers, filter-feeders, suspension-feeders, detritus feeders, microbial loops, herbivores, high-level predators, etc.). *P.oceanica* is a remarkable hot-spot of biodiversity and host more than 20% of the species knowed in Mediterranean (Boudouresque, 2004).

In Provence and in the French Riviera (France, North-Western Mediterranean Sea), *P. oceanica* meadows are particularly developed and provide many ecosystem services (Boudouresque et al., 2012). Special attention is given to this ecosystem by scientists and Marine Protected Areas (MPAs) managers since the 1950s (Boudouresque and Meinesz, 1982; Molinier and Picard, 1952). The Port-Cros National Park, the Calanques National Park and the Côte Bleue Marine Park (Fig. 1) are three MPAs for which the health of *P. oceanica* seagrass meadows is a major issue (Astruch et al., 2012). Both scientists and MPA managers are involved in the monitoring and the management of this coastal ecosystem for which they have developed a specific health index.

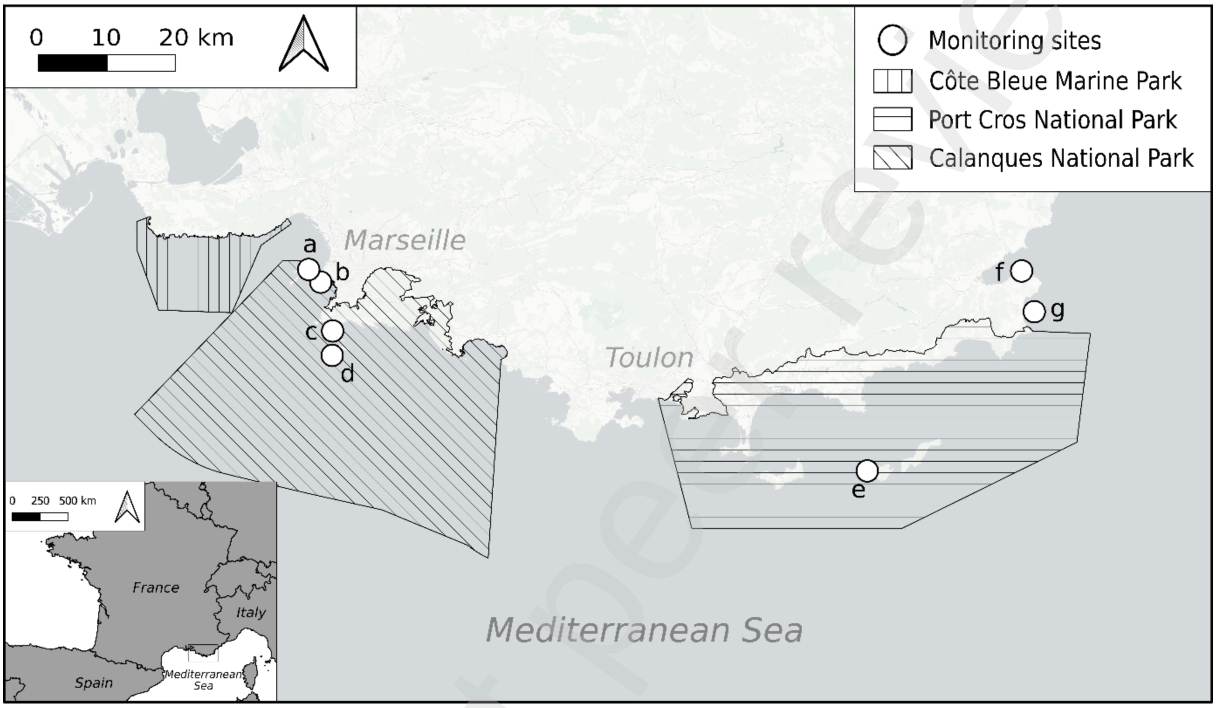


Figure 1: Map of the study area including location of the MPAs[a] and the monitoring sites. (a) Ratonneau island, (b) Rade Sud Marseille, (c) Plateau des Chèvres, (d) Moyades, (e) Port de Port-Cros, mooring area, (f) Canoubiers East, (g) Pampelonne. ([a] Port Cros and Calanques National Parks are both marine and terrestrial protected areas)

A conceptual model of the *P. oceanica* seagrass meadow ecosystem has been proposed by Personnic et al., (2014; Fig. 2) to describe a simplified functioning of ecosystem with functional boxes.

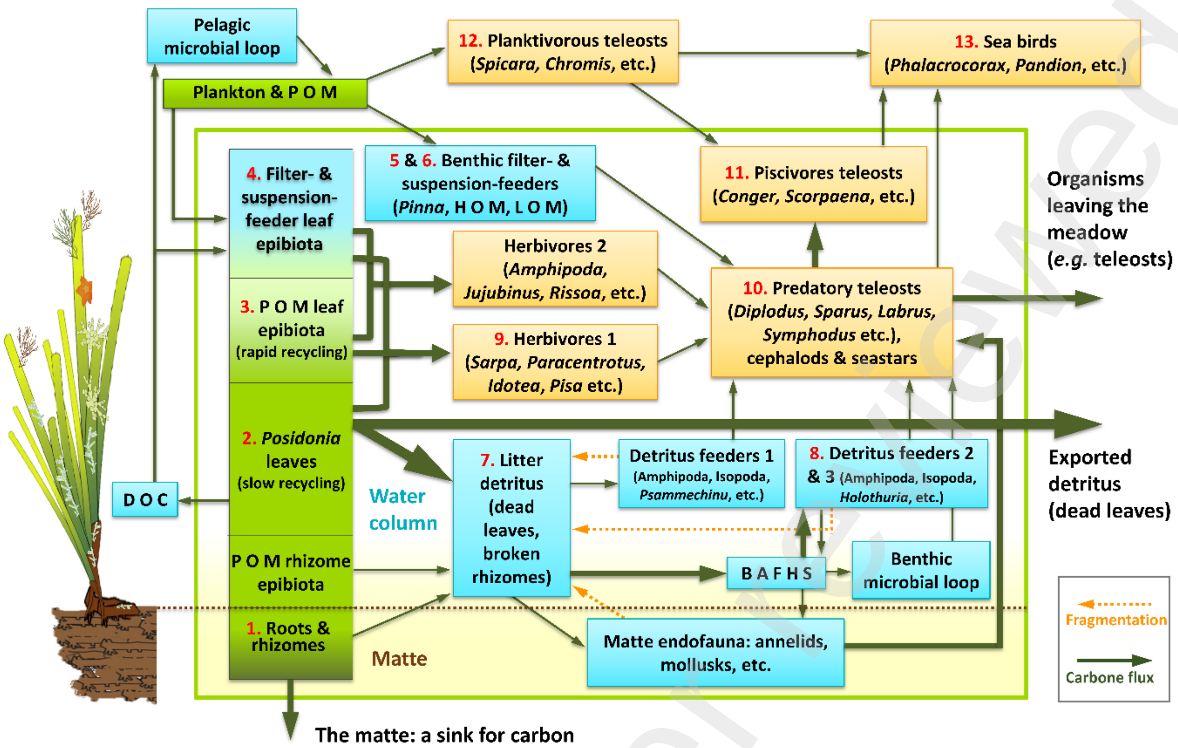


Figure 2: Conceptual model of the functioning of the P. oceanica seagrass meadow ecosystem (adapted from: Personnic et al., 2014) (Numbered boxes correspond to functional compartments included in the EBQI, primary producers are in green; filter-feeders, suspension-feeders, litter, detritus feeders, Dissolved Organic Carbon (DOC) and microbial loops are in blue; predators (including herbivores) are in yellow. The width of the arrows roughly represents the importance of the carbon flow. The proper P. oceanica ecosystem is included within the red rectangle. MPO: Multicellular Photosynthetic Organisms. POM: Particulate Organic Matter, HOM: High level Organic Matter, LOM: Low level Organic Matter, ***BAFHS: Decomposers, namely*** *Bacteria*, *Archaea*, ***Fungi and heterotrophic stramenopiles such as Labyrinthulomycota and Oomycota***).

Protected by Bern (Annex 1) and Barcelona (Annex 2) conventions, *P. oceanica* seagrass meadow has been identified as a priority habitat according to the European Habitat Directive 92/43/EEC on the conservation of natural habitats and fauna and flora (i.e. Habitat Directive). In addition, *P. oceanica* is a strictly protected species in France, since 1988 (Boudouresque and Bianchi, 2013; Pergent, 1991). Because *P. oceanica* meadow is threatened by many drivers of change: cascading effect of predator fishes overexploitation, trawling, anchorages, pollution, coastal development, invasive species, etc. (*e.g.* Boudouresque et al., 2012; Montefalcone et al., 2008; Pergent et al., 2013; Sala et al., 1998; Scheffer et al., 2005). It is considered in inadequate conservation status by the Habitat Directive in some areas in France (Holon et al., 2015; Pasqualini, 1997; Pergent et al., 2019). *P. oceanica* is also listed as an indicator of coastal water quality under the European Water Framework Directive (WFD, 200/60/EC). In coherence with all those protection statuses and under the ecosystem-based approach promoted by the European Marine Strategy Framework Directive (MSFD, 2010/477/EU), Personnic et al., (2014) have proposed an original index for the assessment of *P. oceanica* seagrass meadow quality: the Ecosystem-Based Quality Index (EBQI).

The EBQI has been developed to monitor the ecological conservation status of *P. oceanica* seagrass meadows in support to its management. EBQI goes further a monitoring of *P. oceanica* that would be limited to the plant itself (*e.g.* leaf growth, cover, shoot density) to monitor the entire ecosystem as conceptualized in Figure 1. Its implementation is based on 3 steps: (i) *on-site* measuring of a set of parameters selected to assess the functioning of the different compartments of *P. oceanica* ecosystem (Fig. 2); (ii) determining the EBQI score of each compartment from 0 (Bad) to 4 (Good) based on parameters value; (iii) applying an algorithm to calculate the EBQI score of the entire ecosystem from the weighted sum of the EBQI scores of its composing compartments. For practical purpose the ecosystem EBQI score is finally converted in 0 to 10 scale to determinate the ecological status of the monitored site. The complete methodology is detailed in Personnic et al., (2014).

In our study, we hypothesize that the notation of functional boxes can be a good information to assess the ES capacity of the *P. oceanica* seagrass meadow using a state and transition model.

2.2 State and transition model

A state and transition model is a conceptual and operational framework for organizing and producing information regarding ecosystem dynamics and management (Lavorel et al., 2015). While its scientific application is widespread for some terrestrial habitats, mainly rangelands (Ratcliff et al., 2018) and grasslands (*e.g.* Quétier et al., 2007; Tarrasón et al., 2016), its application in the marine realm remains rare (*e.g.* Kermagoret et al., 2019). In this paper, we adapted the state and transition model as presented in Lavorel et al., (2015) to describe the evolution of the ES bundle provided by *P. oceanica* meadows regarding different drivers of change using field observations in the form of EBQI scores.

Three steps were necessary for building the model (Fig. 3). In the first step, we depicted the system in its initial state, defining its functioning and its capacity to provide ES based on expert consultation. In the second step, we characterized the ecosystem dynamics under transition factors and defined alternative states of the *P. oceanica* seagrass meadow based on expert judgement. For each alternative state, we identified a corresponding site in the study area. In the third step, we determined the evolution of the capacity of the meadow to provide ES in each alternative state based on the EBQI notation of the corresponding site.

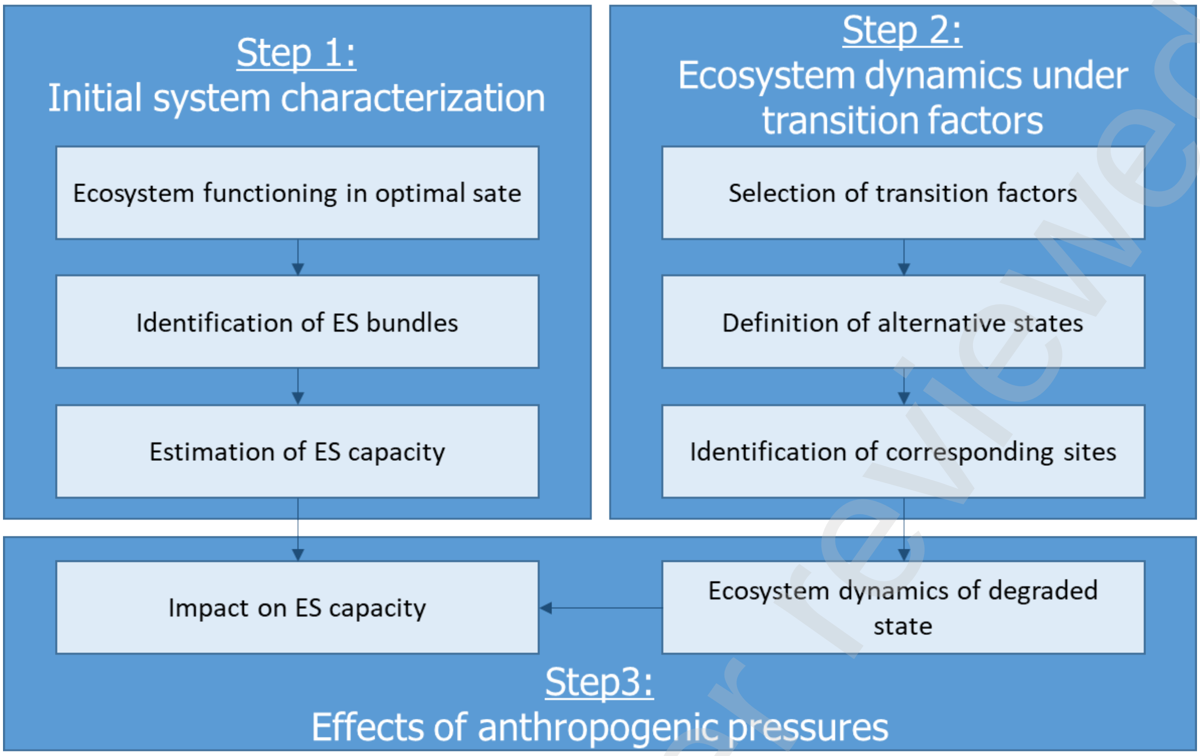


Figure 3: Building of the state transition model. ES: Ecosystem Service.

2.2.1 Step 1: Initial system characterization

In order to define the initial system, we carried out a workshop organized the 2nd of December 2019, completed by bilateral meetings with several scientific and *ex-post* email exchanges. In total, 12 experts, including scientists and managers participated in the consultation and are included in the authors of the present work.

Experts defined the initial system as the optimal ecological state of *P. oceanica* seagrass meadow, *i.e.* the state in which EBQI would take its maximum value (EBQI = 10; Personnic et al., 2014). The ecosystem dynamics in this optimal state is thus described by the conceptual model (Fig. 2).

As our final objective was to be relevant to the local management context, we selected the list of ES provided by the *P. oceanica* seagrass meadow with the local experts (Abson et al., 2014; Scemama et al., 2020)[1]. The process that support the contribution of *P. oceanica* meadows to the provision of the selected ES was then reinforced with scientific literature. The 16 ES provided by *P. oceanica* seagrass meadows in Provence and French Riviera are described in the Table 1.

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[1] The list of the selected ES use a context dependent typology, we propose a correspondence table with the CICES classification system in Supplementary Material.

145 *Table 1: Ecosystem services provided by P. oceanica in Provence and French Riviera (PS: Provisioning Services; CS: Cultural*
146 *Services; RS: Regulating Services; and EF: Ecological Function).*

Label	Ecosystem service	Description and reference	Functional compartment involved in the ES
PS1	Sea urchins fishing	France is considered the largest market for sea urchins in Europe. P. lividus is the favourite species and the Mediterranean fishery its main national provider (Stefánsson et al., 2017). P. oceanica form with rocky substrates (boulders and solid rock) the main habitats for P. lividus in the Mediterranean area (Boudouresque and Verlaque, 2020; Box 9 in Fig. 2).	Density of *P. lividus* (ind.m^{-2}) (parameter used to assess functional box #9).
PS2	Professional fishing	P. oceanica meadows are home to many fish species (Astruch et al., 2018; Francour, 1997; Harmelin-Vivien, 1983, 1982; Ourgaud et al., 2015) of which many are of commercial interest (e.g. Sparids, Scorpanids, Labrids, European seabass, Red Mullet; Leleu et al., 2014).	All fish compartment, more precisely: predatory (#10), piscivorous (#11) and planktivorous teleosts (#12)
CS1	Recreational fishing	Recreational fishing occurs in P. oceanica meadows (Campagne et al., 2015; Scemama et al., 2020). It derives from both the capture of fishes (for the exclusive consumption of the fisherman and his family or released after capture) and broader interactions with the marine environment (e.g. landscape or heritage).	Combination of compartments involved in the provision of urchins (PS1), fishes (PS2) and landscape (CS4).
CS2	Education	P. oceanica is a support of production and dissemination of knowledge for society regarding the functioning of marine ecosystems (Boudouresque and Meinesz, 1982; Campagne et al., 2015; Scemama et al., 2020). P. oceanica has become the symbol of the Mediterranean Sea; its banquettes of stranded dead leaves widely participate in the Mediterranean identity (Oudin and Boudouresque, 2023).	The capacity is associated to the global functioning of *P. oceanica*.
CS3	Research	P. oceanica is the subject to many research project (Campagne et al., 2015). However, the capacity of an ecosystem to support research is not limited to its state, indeed, degraded ecosystems can also trigger research regarding its threat and management (Turner et al., 2014).	Degraded states are further explored by science. This less applies to dead matte.
CS4	Landscape attractivity	P. oceanica meadows constitute elements of underwater scenery, moreover they attract emblematic species appreciated by naturalist. As a result, they contribute to the attractiveness of the marine environment (Thorin et al., 2014).	*P. oceanica* rhizome and leaves (#1-2) and associated macrofauna i.e. benthic species (#5-6), fish (#10-11-12) and birds (#13).

RS1	Coastal protection	The service of coastal protection provided by P. oceanica results from the ability of the plants (i) to reduce the hydrodynamics of waves and current (Stratigaki et al., 2011), (ii) to produce biogenic sediment (the so-called 'sand factory'), a part of which is exported to beaches during storms (De Falco et al., 2017; Martín Prieto et al., 2018; De Luca et al., 2020), (iii) to accumulate and stabilize sediments during the settlement of the matte (Boudouresque et al., 2016; De Falco et al., 2000). We have to underline that the role of the banquettes formed by detritus of P. oceanica stranded in beaches stabilization (Rotini et al., 2020) is not integrated in this assessment.	*P. oceanica* rhizome and leaves (#1-2).
RS2	Turbidity regulation	P. oceanica promotes sediment accretion by increasing deposition and buffering resuspension and thus contributes to turbidity regulation (Gacia et al., 1999).	All the plant and its epibiota (#1-2-3).
RS3	Contaminant regulation	This service results from the concentration of contaminants from the marine environment: organic and inorganic contaminants can be accumulated in the plant (Pergent et al., 2011) or trapped into the sediments (Bonanno and Di Martino, 2017).	Elements that capture contaminants i.e. the plant and its biota and the necromass (#1-2-3-7).
RS4	Climate regulation	The service of climate regulation is the capacity of P. oceanica to store and sequester carbon in the long run; as a result, it contributes to the compensation of anthropic greenhouse gas emissions (Pergent-Martini et al., 2021).	All photosynthetic elements of *P. oceanica* meadows (#1-2-3) and the litter detritus (#7).
EF1	Export of Organic Matter (OM)	This service designates the part of P. oceanica biomass production that is exported to other ecosystems where it can support the provision of other ecosystem services (e.g. coastal protection by banquettes of dead leaves stranded on beaches) (Oudin and Boudouresque, 2023). This service, unusual as regard to ecosystem services approach, is essential to capture the importance of the interaction of P. oceanica meadow with surrounding ecosystems (Boudouresque et al., 2016). Only 3% to 10% of P. oceanica primary production of biomass is directly consumed (Pergent et al., 1997). The remaining part accumulates in detritus made of leaves, roots, rhizomes and indigenous epibiota and constitutes the necromass (Boudouresque et al., 2016). Between 10 and 55% of this necromass is exported to adjacent ecosystems (beaches, rocky substrates of the sublittoral, circalittoral and bathyal ecosystems).	The litter detritus (#7) and its constituting elements (#1-2-3).
EF2	Shelter	P. oceanica meadows constitute important habitats for many species, with their leaves that can reach	All elements constituting of *P.*
EF3	Nursery		

		over 1 m high, they provide shelter against predation, they can sustain the development of juveniles of many species, providing an essential habitat and they form spawning areas (Francour, 1997; García-Rubies and Macpherson, 1995; Jiménez et al., 1996).	*oceanica* plant, i.e. rhizomes, leaves and associated litter detritus (#1-2-7).
EF4	Spawning ground		
EF5	Primary production	P. oceanica meadows constitute important contributors to primary production (Pergent-Martini et al., 1994). The production of organic matter from photosynthesis in the ecosystem (by the plant or the associated epibiota) that transforms mineral carbon into organic carbon, is at the basis of the functioning of trophic networks.	All photosynthetic elements of *P. oceanica* meadows (#1-2-3-7).
EF6	Secondary production	The primary production supports an important trophic network of herbivorous such as teleosts (Sarpa salpa), sea urchin (Paracentrotus lividus), crustaceans (Idotea spp. and Pisa spp.), detritus feeders such as Amphipoda, Isopoda etc. (see Figure 1; Personnic et al., 2014).	All animal species, i.e. filter- and suspension feeders (#4-5-6), detritus feeders (#8), fishes (#9-10-11-12) and birds (#13).

To assess the capacity of *P. oceanica* seagrass meadow to provide the ES bundle in the optimal state, we questioned the experts by email exchanges. More specifically, we asked the experts to fill in a scoring matrix in which they must answer the question: "What is the capacity of the *P. oceanica* seagrass meadow, in its optimal state (EBQI = 10), to provide ES?" by assigning a score between 0 (zero capacity) and 5 (very high capacity) for each ES. The assessment of ES capacity corresponds to the average of the scores assigned by the experts.

2.2.2 Step 2: Ecosystem dynamics under transition factors

We characterized the effects of anthropogenic pressures on the system based on the same expert consultation than for the initial system characterization. During the workshop, the experts have chosen to define degraded states in light of the different pressures which apply on it (cascading effect of fish overexploitation, fragmentation, pollution, colonization by non-native species). The selection of these states come from the local concern regarding the conservation of *P. oceanica* seagrass meadow (Scemama et al., 2020). We described the states and the transition factors qualitatively based on the discussions resulting from the experts' consultation and then validated by them.

For each of the degraded states we seek to identify sites which would be characteristic of this state and for which an EBQI score would be available. Thus, data from these different sites could be retrieved for the last year available and at 3 levels: at the site level (EBQI of the site, between 0 and 10); at the functional box level (status of the compartment, between 0 and 4); at the functional trait level (parameter value).

2.2.3 Step 3: Effects of anthropogenic pressures

The quantification of the ES capacity in the degraded state was then carried out by crossing the data obtained from the expert consultation and from the data of EBQI of the corresponding sites. For each degraded state of *P. oceanica*, we described the system according to the actual state of its correspondence site.

We identified the functional compartment of the meadow involved in the ES production (Table 1; Fig. 2). Then, they determined whether the available data collected for EBQI were good indicators to assess the ecosystem capacity to produce ES and at which level the data should be mobilized (site, compartment or parameter). The last step consisted in calculating the ES capacity in degraded states with regard to the ES capacity in the optimal state and in connection with ecological monitoring data. The calculation of the ES capacity is defined according to the following generic equation.

$$ES_{ds_j} = \frac{V_{ds}}{V_{os}} \times ES_{os_j} \qquad \text{(Eq. 1)}$$

Where: ES_{ds_j} the level of the ecosystem service capacity j in the degraded state ds; V_{ds} the value of the data used to assess the ecosystem service capacity *j* in the degraded state ds; V_{os} the value of the data used to assess the ecosystem service capacity *j* in the optimal state os; ES_{os_j} the level of the ecosystem service capacity j in the optimal state os.

The functional processes underlying ES provision are different for each ES, we first identified the compartment of the *P. oceanica* involved in ES provision with the experts (Table 1). The Table 2 summarizes the level of information used to assess ES capacity. Most ES are directly linked to compartments of the ecosystem. In those cases, the value used to assess the ES capacity is based on the mean value of the EBQI score of the compartments involved in the ES provision. In other cases, detailed hereafter, we had to use the EBQI monitoring at another level than the compartment or adopt a special convention.

In some cases, the relevant indicator was to use the EBQI at another level than the compartment score. The ‘provision of sea urchins’ (PS1) obviously involve compartment #9 (herbivores in Fig.2) which is monitored by the density of *P. lividus* (individuals.m^{-2}) and a grazing index of the salema *Sarpa salpa* (% of leaves grazed by *S. salpa*). However, the EBQI score for compartment #9 is maximum for an average density of urchins, if density gets too high the EBQI score drop to 0 reflecting an issue in the ecosystem functioning. However, such imbalance would benefit to the associated ES. As a result, we rely on the direct monitoring of the parameter ‘density of *P. lividus*’ to assess the ‘provision of sea urchins’ capacity.

In the case of ‘education’ service (CS2), it is difficult to identify a specific compartment involved in the provision of the service, we rather argue that the capacity is associated to the global functioning of *P. oceanica*. As a result, we use the global EBQI score to assess this ES.

In the case of ‘research’ and ‘recreational fishing’ services, we had to establish special conventions, as the provision of ES does not stem directly from ecological processes. Firstly, regarding “Research” ES (CS3), the link between the state of the ecosystem and the level ES it provides is not obvious. Indeed, this link can be both positive and negative, meaning that threats to ecosystems provide research opportunities just as ecological richness (Mongruel et al., 2019; Turner et al., 2014) to the extent that current research in ecology is also geared towards understanding links between pressures and ecological states (*e.g.* DPSIR approach; Pinto et al., 2013). As a result, we considered that a degraded state will be further explored by science. In contrast, the degraded dead matte state remains much less investigated by science.

Secondly, “Recreational fishing” ES (CS1) also have an ambiguous link to the state of the ecosystem. The quantity of fishes or urchins is not the only factor that motivates recreational fishermen. Martin et al., (2018) show that recreational activities (including recreational fishing) results from the practice of sport in combination with the benefits from fish provision and seascape ES. As a result, we consider that the score for Recreational fishing ES results from the combination of the scores of other ES, namely “Urchins” (PS1), “Fishes” (PS2) and “Landscape” (CS4) ES.

Table 2: Level at which the data have to be mobilised for each ES (Boxes numbers refer to the functional boxes in Fig. 2).

LABEL	ECOSYSTEM SERVICE	EBQI GLOBAL	EBQI BOX	PARAMETER	COMPARTMENT OR SERVICE
PS1	Sea urchins fishing			X	(Box 9) Density of *P. lividus* (ind.m^{-2})
PS2	Professional fishing		X		Boxes 10, 11 and 12
CS1	Recreational fishing				Combination of PS1, PS2 and CS4
CS2	Education	X			All
CS3	Research				Convention
CS4	Landscape attractivity		X		Boxes 1, 2, 5, 6, 9-12, 13
RS1	Coastal protection		X		Boxes 1 and 2
RS2	Turbidity regulation		X		Boxes 1, 2 and 3
RS3	Contaminant regulation		X		Boxes 1, 2, $3^{(1)}$ and 7
RS4	Climate regulation		X		Boxes 1, 2, $3^{(1)}$ and 7
EF1	Export of Organic Matter (OM)		X		Boxes 1, 2, $3^{(1)}$ and 7
EF2	Shelter		X		Boxes 1, 2 and 7
EF3	Nursery		X		Boxes 1, 2 and 7
EF4	Spawning ground		X		Boxes 1, 2 and 7
EF5	Primary production		X		Boxes 1, 2, $3^{(1)}$ and 7
EF6	Secondary production		X		Boxes $4^{(1)}$, 5, 6, 8, 9, 10, 11, 12 and 13

[1] : As indicator is measured per shoot, contribution of box 3 and 4 to ES provision is proportionate to shoot density (*i.e.* box 2).

3 Results

3.1 Step 1: Initial system characterization

- Ecosystem dynamics of optimal state and identification of ES bundle

The optimal ecological state of *P. oceanica* meadow (EBQI = 10) remains theoretical insofar as it is not actually observed, since this ecosystem suffers a more or less intense anthropogenic impact everywhere. This state is nonetheless potential, *i.e.* realistic. This state is mainly characterized by a high density of *P. oceanica* leaves (≥ 490 shoots m^{-2}) with a medium biomass of epibionts (≥0,3 to <0,8 g DM shoot^{-1}), a large biomass of fish, an medium density of herbivorous sea urchins *Paracentrotus lividus* (≥1.0 to <5.0 individuals m^{-2}), etc.

- Assessment of ES capacity

Based on an expert scoring, the capacity of *P. oceanica* meadow to provide the ES bundle in the optimal state varies depending on the type of ES (Figure 4).

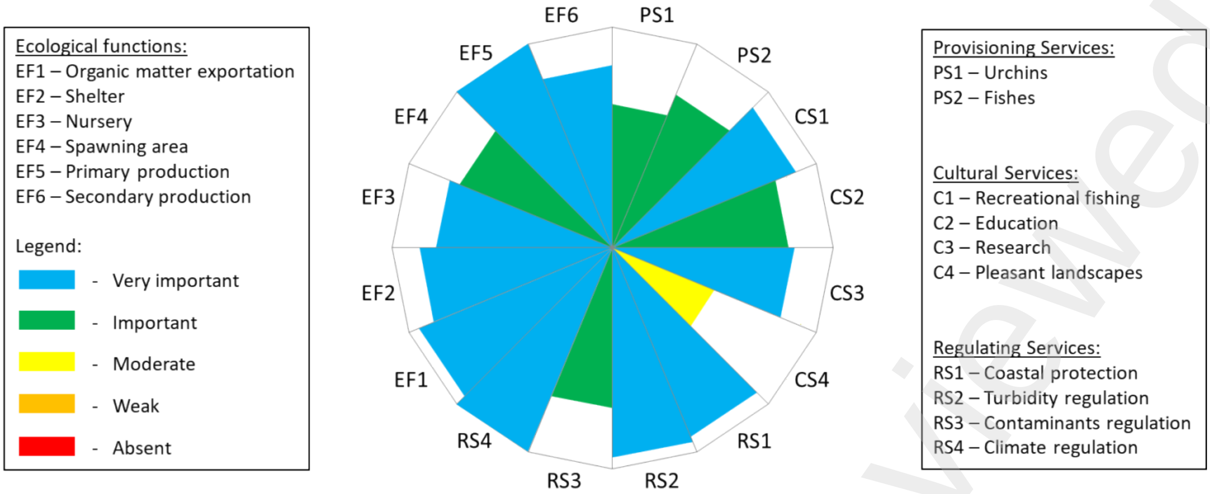


Figure 4: Ecosystem services capacity for the optimal state of P. oceanica seagrass meadows.

3.2 Step 2: Ecosystem dynamics under transition factors

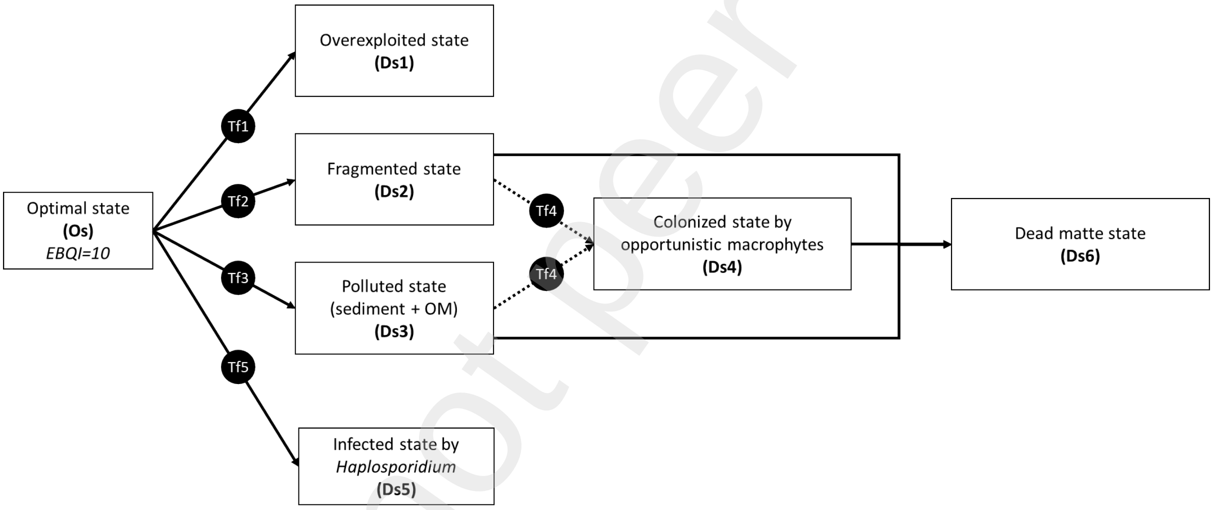


Figure 5: Different states of P. oceanica ecosystem under different transition factors.

We defined six degraded states (Ds1 to Ds6) that are source of concern for *P. oceanica* conservation regarding the pressures exerted on them, *i.e.* transition processes (Tf1 to Tf5).

- **Overexploited state (Ds1)** in which fishes stocks (particularly invertivorous and top-predators) are depleted;
- **Fragmented state (Ds2)** within which the surface of the seagrass and its connectivity is interrupted by non-vegetated areas in the form of patches or scares;
- **Polluted state (Ds3)** by water inputs in which the seagrass is subjected to hypersedimentation, eutrophication and increased turbidity;
- **State colonized by opportunistic invasive macrophytes (Ds4)** such as caulerpes (*Caulerpa taxifolia* and *C. cylindracea*) or *Lophocladia trichoclados* that compete with *P. oceanica*;

- **Infected state by *Haplosporidium pinnae* (Ds5)**, pathogen of pen shell *Pinna nobilis*, which leads to massive mortality of this large bivalve mollusk.
- **Dead matte state (Ds6);** it constitutes a semi-hard to hard habitat, on which many species of macroalgae thrive. The substrate, formed by a tangle of dead roots and rhizomes, blocked by elements of very heterogeneous grain size, from fine gravel to silt, can be particularly compact and favours the establishment of a relatively specialized fauna.

- Correspondence with monitored sites

Given the identified transition factors and associated degraded states, we identified seven monitored sites as being able to correspond to the degraded states defined in the model (Table 3 and Fig. 1).

Table 3: Correspondence between degraded states and monitored states.

DEGRADED STATES	CORRESPONDING MONITORED SITES	YEAR OF THE MONITORING	EBQI SCORE	CONFIDENCE INDEX (%)	ES LOSS INDEX (%)
OVEREXPLOITED STATE (DS1)	Rade Sud Marseille	2018	5	100	29%
FRAGMENTED STATE (DS2)	Canoubier East Port de Port-Cros, mooring area	2015 2015	4.1 4.9	85 83	46% 38%
POLLUTED STATE (DS3)	Plateau des Chèvres	2018	3.9	100	40%
COLONIZED STATE BY OPPORTUNISTIC MACROPHYTES (DS4)	Pampelonne(1)	2022(1)	3.7	100	54%
INFECTED STATE BY HAPLOSPORIDIUM (DS5)	Moyades	2019	5.8	97	25%
DEAD MATTE STATE (DS6)	Ratonneau island	2020	1.7	100	84%

(1) The monitoring of pampelonne site for colonization by opportunistic macrophytes has been conducted after the massive infection of p. nobilis by h. pinnae. In order to ignore this impact we replace the value for p. nobilis monitoring in this site by a value obtained from a neighbour site with similar condition and measured before the infection.

3.3 Step 3: Effects of anthropogenic pressures

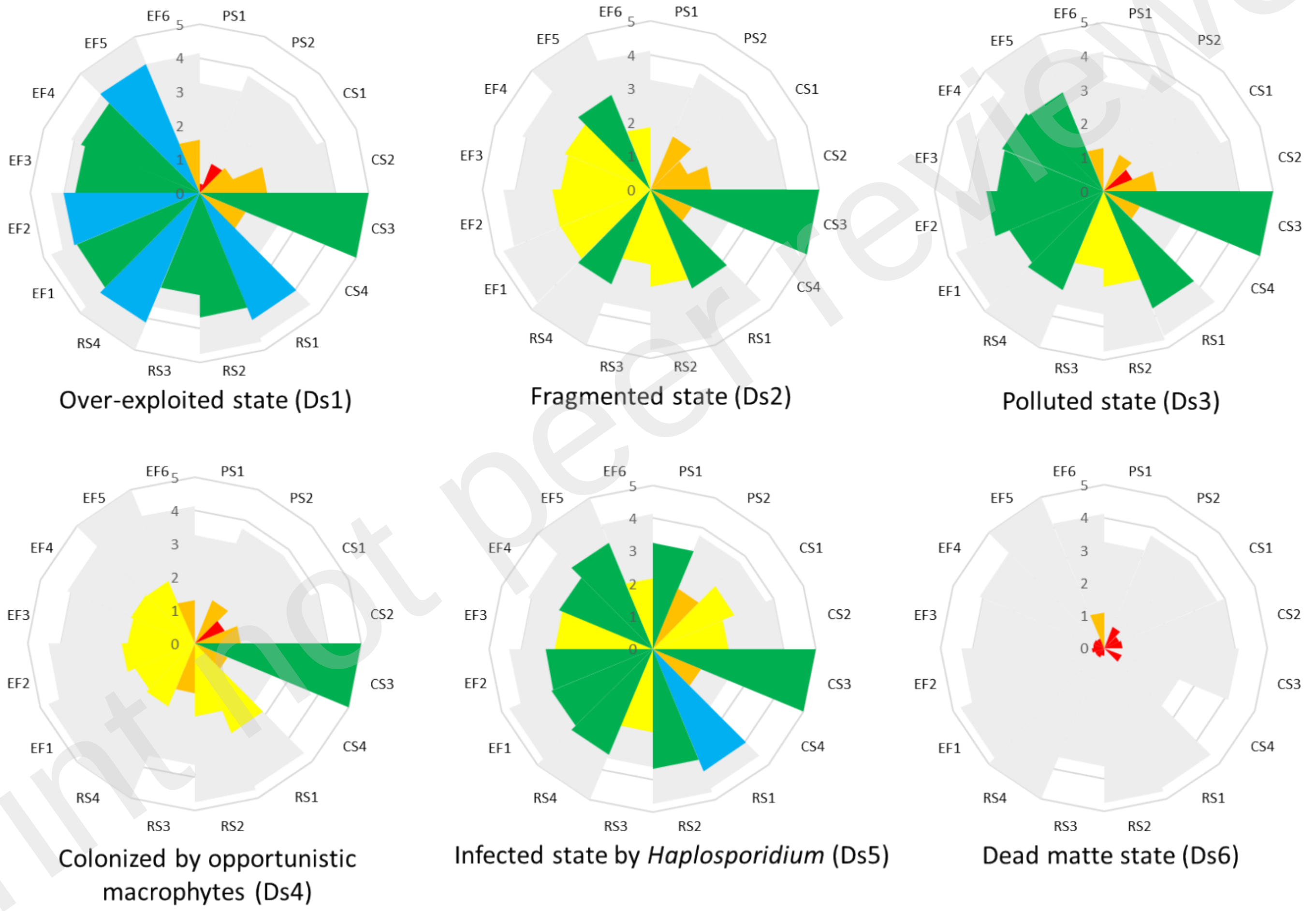
Provisioning Services:
PS1 – Urchins
PS2 – Fishes

Cultural Services:
CS1 – Recreational fishing
CS2 – Education
CS3 – Research
CS4 – Pleasant landscapes

Regulating Services:
RS1 – Coastal protection
RS2 – Turbidity regulation
RS3 – Contaminants regulation
RS4 – Climate regulation

Ecological functions:
EF1 – Organic matter exportation
EF2 – Shelter
EF3 – Nursery
EF4 – Spawning area
EF5 – Primary production
EF6 – Secondary production

Legend:
🟦 - Very important
🟩 - Important
🟨 - Moderate
🟧 - Weak
🟥 - Absent



Over-exploited state (Ds1)

Fragmented state (Ds2)

Polluted state (Ds3)

Colonized by opportunistic macrophytes (Ds4)

Infected state by *Haplosporidium* (Ds5)

Dead matte state (Ds6)

Figure 6: ES capacity of P. oceanica seagrass meadow in different degraded state. The light grey indicates the Optimal state.

Results of the calculation of the ES capacity bundle of *P. oceanica* meadows in the different degraded states are presented in Fig. 6. In order to facilitate the reading of the results, we created an ES loss index that allows a rapid understanding of the loss of ES (Table 3). ES loss index is the difference between the ES bundle in the reference state and the ES bundle in the degraded state expressed in percentage.

4 Discussion

4.1 A decrease in the ES bundle in degraded states

Generally, degraded states are associated to a degraded ES bundle, illustrating the impacts of anthropogenic pressures on the capacity of *P. oceanica* ecosystem to provide ES. Moreover, it shows how much degradation trends can affect ES capacity. Indeed, in the dead matte state (Ds6), almost all functional compartments have disappeared; as a result, the habitat becomes unable to provide any of the usually provided ES. The dead matte state seems to correspond to a regime shift in the seagrass trajectory, as stressed by Montefalcone et al., (2007), as no ES usually provided by the meadows are present (loss of 84% of ES). In this way, it may not be relevant to assess its ES bundle with the same lens as *P. oceanica*. But it would also not be relevant to exclude dead matte from the ecosystem, as dead matte is a structural element (in addition to a functional compartment) or the *P. oceanica* ecosystem; this element is naturally present in most meadows (Boudouresque et al., 2021b, 2009).

Provisioning services (PS1 and PS2) are particularly impacted for every studied transition factors. Provisioning services are even impacted when *P. oceanica* meadows are exposed to pressures that are not supposed to affect the compartment responsible for the service. This is notably the case of the "Infected state by *Haplosporidium*" (Ds5) as it only affects *Pinna nobilis*, that are located in functional compartment #5 and not involved in provisioning services. This result reflects the fact that overfishing in the Mediterranean Sea is ubiquitous and has greatly impacted fish biomass (Boudouresque et al., 2017; Vasilakopoulos et al., 2014). In this perspective, there is no site that can really be considered as completely unaffected by exploitation, even in restricted or protected areas.

In few cases, habitat degradation can increase the provision of ES. It is notably the case of the research (CS3). Research interest is higher for degraded states as the understanding of the relationships between pressures and ecological states receive more and more attention. This trend may be even more important regarding the priority conservation status of *P. oceanica* with regards to the Habitat Directive. The provision of sea urchins (PS1) could also theoretically increase in overexploited sites because of the disappearance of its predators under fishing pressure (*e.g.* mainly sparids and *Coris julis*). However, the illustrative site for overfishing (namely "Rade Sud de Marseille") shows a decrease in both fishes and urchins. This may be linked to a global overexploitation of commercial species in the area, targeting fishes and urchins (Melis et al., 2019; Ourgaud et al., 2015).

4.2 Transition factor in the studied area

Overexploitation by fishing (Tf1) - In the French Mediterranean Sea, 80% of fishing activities are carried out in very coastal areas (Mongruel et al., 2019). But at the scale of the *P. oceanica* seagrass meadow of the Côte Bleue Marine Park, small-scale artisanal fishing (*i.e.* vessels less than 12 meters) mainly targets sea bream (*Sparus aurata*), seabass (*Dicentrarchus labrax*), red mullet (*Mullus surmuletus*) and scorpion fish (*Scorpaena spp.*) (Leleu et al., 2014) while inshore trawl fishing (*i.e.* vessels of 12 to 19 meters) also catches non-target species (Boudouresque et al., 2017). The depletion of fishes stocks (particularly invertivorous and top-predators) can lead by a cascading effect, to an overgrowth of sea urchins (*Paracentrotus lividus*) and Salema (*Sarpa salpa*) populations and therefore to overgrazing seagrass (Boudouresque et al., 2017; Sala et al., 1998; Scheffer et al., 2005). Current knowledge does not make it possible to define a maximum sustainable yield (MSY) beyond which we would go from sustainable exploitation of the resource to overexploitation.

The qualitative and / or quantitative degradation of habitats (Tf2) – (i) *P. oceanica* is particularly vulnerable to trawling (Boudouresque et al., 2009). A standard trawler would uproot between 99,000 and 363,000 shoots per hour (Martín et al., 1997). To limit this impact, a regulation prohibits trawling in the 3 nautical mile zone (around 5.8 km). However, this regulation remains little respected up to recently. Trawling is believed to be responsible for the loss of 12% of the seagrass area in Corsica (Pasqualini et al., 2000). The time required for the total recovery of the meadow after trawling is estimated around 100 years (González-Correa et al., 2005). (ii) The impact of anchoring by large ships, especially yachts and cruise ships, in sheltered Mediterranean bays is obvious (Montefalcone et al., 2008; Pergent-Martini et al., 2022). For example, near Porquerolles, the anchoring of these boats generated scars 1 to 2 m wide and up to 296 m long, generating an area of dead mat equal to 4.2 ha (Boudouresque et al., 2009). More recently, a study in Corsica showed that boat anchoring between 2019 and 2021 impacted the general state of conservation of *P. oceanica* meadows and generated a regression of 14.7% of their surface in the study area (Pergent-Martini et al., 2022). The anchoring of small pleasure boats also generates uprooting of *P. oceanica* shoots (for example, 68 000 shoots per hectare in an area of 1.4 ha at Elbu Cove in Corsica [unpublished data from authors]). However, the seagrass impacted by this type of anchoring remains capable of producing new shoots each year. Anchoring by these small boats induces a relative limited threat compared to that of larger boats. The maximum sustainable mooring pressure would be 2 mooring events per hectare per day (on average over a year) and should not exceed 10 mooring events per hectare for a given day (Boudouresque et al., 2012). Note that anchor chains in mooring areas cause much more damage than the anchors themselves. (iii) On coasts exposed to strong winds, storm surges and tidal currents, sediment movements can bury seagrass shoots, expose roots and rhizomes and even uproot whole plants (Frederiksen et al., 2004). Infantes et al., (2011) estimate that young shoots of *P. oceanica* need more than half the length of the root to be anchored in the sediment so as not to be dislodged.

Pollution (eutrophication, hypersedimentation, turbidity) (Tf3) – (i) A decrease in *P. oceanica* seagrass meadow quality is observed near large urban centers and Mediterranean wastewater outlets, in particular in the bay of Marseille and surrounding (Boudouresque et al., 2009). Eutrophication, hypersedimentation and increased turbidity largely explain this decrease. This pollution has been decreasing due to improved wastewater treatment (Derolez et al., 2020; Ourgaud et al., 2015). Thus, in the bay of Marseille, a recovering meadow has been identified (Boudouresque et al., 2021b; Pergent-Martini et al., 1995) but it should be noted that this recovery remains relatively slow (a few cm / year). (ii) Fish aquaculture generates pollution linked to the food not consumed and to the fish excrement which accumulates there. In addition, the shade of the cages and the turbidity lead to a reduction in the light intensity necessary for the proper development of *P. oceanica* (Boudouresque et al., 2020c, 2009; Pergent-Martini et al., 2006).

Colonization by opportunistic macrophytes (Tf4) - The Mediterranean Sea is known to be one of the most invaded sea in the world, particularly in the Eastern part (Boudouresque and Verlaque, 2012; Katsanevakis et al., 2016). Here, we considered the colonization by opportunistic macrophytes. At least 5 species of macrophytes can compete with *P. oceanica* (Boudouresque et al., 2009): 2 species of Australian chlorophytes (*C. taxifolia* and *C. cylindracea*) and 3 species of Indo-Pacific rhodophytes (*Acrothamnion preissii*, *Lophocladia trichoclados* (previously referred to as *L. lallemandii*) and *Womersleyella setacea*). The first two are known to have a significant impact on the meadow along the French coasts (Klein and Verlaque, 2009; Ruitton et al., 2005), so we have focused on these species. We have to note that this colonization is limited when the *P. oceanica* meadow is in good health (i.e. high shoot density and cover, etc.); this is why we choose to consider it as an additional transition factor that comes after the meadows has already been impacted (Fig. 5). Because of the current climate change and the warming of the Mediterranean combined with human activities, new species are reaching and settling within the Mediterranean Sea. Recently, the Asian Phaeophyceae *Rugulopteryx okamurae* is spreading in Bay of Marseille and surrounding (Ruitton et al., 2021).

Infection by *Haplosporidium* (Tf5) - *Haplosporidium pinnae* epidemic affecting pen shell *Pinna nobilis* has started in 2016. This epidemic caused the death of 99% of the population on the Spanish coasts (Catanese et al., 2018). Since then, the epidemic has continued to spread throughout the

Mediterranean Sea, the Balearic Islands, Corsica, Provence and French Riviera (Ruitton and Lefebvre, 2021). A mortality rate over 99% is now observed, so that *P. nobilis* is now considered as critically endangered by the UICN Red list (Kersting et al., 2019).

What about the climate change? Most of the impacts of climate change on marine and coastal ecosystems remain uncertain. These effects are also multiple and linked to different factors (warming of marine waters, acidification, sea level rising, increase in frequency and intensity of extreme events, etc.) (Pergent et al., 2014). For example, the *P. oceanica* seagrass meadow constitutes the "climax" ecosystem over a large part of the Mediterranean coastal areas in shallow water. With the warming of marine waters, two other macrophytes present in the Mediterranean Sea, namely *Cymodocea nodosa* and, to a lesser extent, *Zostera noltei* could constitute pioneer species in the succession, allowing the colonization of *P. oceanica* seagrass meadow (Boudouresque et al., 2009). However, meadows could also be replaced by non-indigenous species (NIS). A substitution of species by less structuring species can trigger profound changes within the associated communities. For example, the invasive Magnoliophyta *Halophila stipulacea* has been found along French riviera in the bay of Cannes (Thibaut et al., 2022). However, some authors hypothesize that *P. oceanica* would be able to adapt by modifying its thermal optima (Cantasano, 2023), as it is a phenomenon already observed in terrestrial plant species (Koch et al., 2013). These different prospective scenarios highlight the uncertainties linked to the effects of climate change. In this study, we limit the consideration of climate change to the idea that it can lead to an intensification of certain transition factors described above (example of fragmentation linked to extreme events). However, the impact of climate change may lead to the apparition of new transition factors such as other NIS that would benefit from warming of marine waters to continue their northward migration. We can take the example of the rabbitfish, *Siganus rivulatus* and *S. luridus*, which was raised as potential future threat by local MPA managers (Scemama et al., 2020). Rabbitfish fishes are so-called "Lessepsian" species, i.e. species which took advantage of the opening of the Suez Canal (1869) to migrate from the Red Sea to the Mediterranean. Rabbitfish fishes proliferate particularly along the Eastern basin coasts (Hassan et al., 2003), and continue their colonization towards the north and the west. The first specimens of *S. luridus* were observed on the French coast within Côte Bleue Marine Park in 2008 (Daniel et al., 2009), without proliferating. A second species of rabbitfish *S. rivulatus* was recorded in 2018 near Côte Bleue (Iglesias et al., 2020). To date, it therefore constitutes a potential threat for the French coasts.

4.3 Reference state

To calculate the ES profile of *P. oceanica* seagrass meadow under different pressures we used a hypothetical reference state where EBQI is the highest (ES_{os_j} in Eq. 1). However, this state remains theoretical insofar as it is not really observed in the French Mediterranean, where every coastal ecosystems suffer an anthropogenic impact, more or less intense, even in the most effective protected areas. This can lead to issues in characterizing the impacts of a selected factor of change on *P. oceanica* seagrass meadow's ES capacity as it can integrate trends that are more global and that may affect all sites simultaneously through cascading impacts on biodiversity and ecosystem functioning. (i) For example, in 'recent' human history (one century), the Mediterranean Sea has always been exposed to a high fishing pressure (Coll et al., 2010). Today, it is one of the FAOs fishing areas with the lowest percentage (36.6%) of stocks fished at sustainable level (FAO, 2022; p. 51). This systematic fishing pressure has a global impact on species diversity (Veloy et al., 2022). Farriols et al., (2017) even showed that an increase of fishing impact could only be detectable where fishing pressure have remained relatively low. (ii) Another example concerns the eutrophication issue. Today, many coastal areas in the north-western Mediterranean sea are currently more and more exposed to oligotrophication as a result of both climate change (Agusti et al., 2017) and a decrease of nutrient inputs associated to the improvement of wastewater treatment (Derolez et al., 2020). Such changes in the nutrient loading in coastal areas has impacts on the fish community of *P. oceanica* seagrass meadows (Ourgaud et al., 2015).

These global trends have impacts on indicators that are used in the EBQI and can lead to misestimate the impact of a factor of change on ES bundle following our approach. For example, in all our selected sites, the density of the sea urchins *Paracentrotus lividus* is very low (close to 0). The assessment of *P. lividus* stocks is a sensitive question because of its high economic value. According to professional urchin harvesters, stocks are depleted in the area whereas scientists advocate that the idea of high quantity of *P. lividus* in the Mediterranean is more likely to reflect of its poor ecological status associated to organic pollution and over-exploitation of their predators (Boudouresque and Verlaque, 2020; Sala et al., 1998). A scarcity of *P. lividus* may be closer to the natural situation as it is observed in the National Nature Reserve of Scandola in Corsica (Boudouresque et al., 2021c). In the end, this debate questions the weight of this box in the calculation of the *P. oceanica* seagrass meadow ES bundle.

The question of an existing reference state for *P. oceanica* is not easy to answer. The highest EBQI score observed in the study area was on the southern coast of the Island of Port Cros where it reached the score of 9.3 (Personnic et al., 2014). We could consider this site to be a better reference state than a theoretical one. However, the difference with the theoretical one is not important (0.7 on global EBQI score) while the level of confidence is very low (CI = 39.3%). In this perspective, we consider that in the purpose of this paper it would bring more uncertainty than relevant information.

4.4 Perspectives

There are several purposes that can justify to implement an ES assessment (Boudouresque et al., 2021a; Harrison et al., 2018; Laurans et al., 2013). In order to maximise their operationalization, several studies underlined the need to adapt the assessment to the targeted decision context (Honey-Rosés and Pendleton, 2013; Marre and Billé, 2019; Scemama et al., 2022). For example, (Saarikoski et al., 2018) suggest that close interaction between researchers, practitioners and stakeholders contribute to conceptual learning, thus facilitating putting ES knowledge in practice. This research fits within these recommendations, indeed the research question resulted from a collaborative work between MPA managers and researchers in the area who chose to target *P. oceanica* given the multiple threats they are exposed to (Scemama et al., 2020). *P. oceanica* meadows are defined as a conservation priority in the area opening the operational scope of the study. We see several potential uses: support MPA managers, raise stakeholder's awareness and supply the development of ecological accounting.

ES assessment can be used by managers to measure conservation outcomes. International certification on management and governance quality is an objective of the French national strategy for protected areas (MTE, 2021). In 2018, the Côte Bleue Marine Park has received the IUCN 'Green-List' label that recognize the fair and effective nature conservation results in protected and conserved areas. The process implies a re-assessment of labeled protected areas every five years. In 2023, managers of the Côte Bleue Marine Park has used ES to report the conservation outcomes. Our approach that allows to establish a direct link between pressures and ES is then useful to managers.

This research offers a synthetic representation of the effect of different threat on the ES bundle of *P. oceanica* (Fig. 6); in this perspective it has a good potential to be used to raise stakeholders' awareness in biodiversity conservation context (*e.g.* MPA's steering committees). Raising awareness is one of the main advantages of the concept of ES (Dick et al., 2018). Indeed, the concept of ES allows a certain interpretative flexibility that allows their conceptualization to be vague in general (*e.g.* food provision, climate regulation) while specific in local use (as applied in this work). This makes ES a good boundary object useful to integrate diverse form of knowledge across social groups and organisational of institutional scales (Steger et al., 2018).

International policies lead States to better integrate the natural capital and the associated ecosystem services (*e.g.* IPBES, EU Biodiversity Strategy). In this study, we propose a methodology which aim to help connecting an existing ecological monitoring index – here the EBQI applied for *P. oceanica* ecosystem (Personnic et al., 2014) – with the ES assessment framework. In this perspective, assessment of the capacity of ecosystems to provide ES could be systematically implemented and used to communicate with decision makers. This approach can also provide information that can be used to provide information to natural capital accounting at the national level following the recommendation of the United Nation's System of Environmental-Economic Accounting (United Nations, 2021).

EBQI or at least the ecosystem-based approach has already been developed for other marine habitats of communitary interests such as underwater marine caves (Rastorgueff et al., 2015), rocky photophilous reefs (Thibaut et al., 2017), coastal detrital bottoms (Astruch et al., 2023) and is under development for coralligenous habitats (Boudouresque et al., 2020b; Ruitton et al., 2014), and saltmarshes (Astruch et al., 2020; Boudouresque et al., 2020b). As a result, this approach could be implemented at larger scale on other habitats for an holistic and global approach to give a more comprehensive look at the condition of marine ecosystems to support human activities in the region.

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